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DOI: https://doi.org/10.1017/s0266467421000122

Journal of Tropical Ecology

www.cambridge.org/tro

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Research Article

Cite this article: Reyes-Chávez J, Quail M, Tarvin S, Kessler M, and Batke SP. Nowhere to escape – Diversity and community composition of ferns and lycophytes on the highest mountain in Honduras. *Journal of Tropical Ecology* https://doi.org/10.1017/S0266467421000122

Received: 27 November 2020
Revised: 6 April 2021
Accepted: 10 May 2021

Keywords:
Altitudinal gradients; Celaque; Central America; climate change; cloud forest; epiphytes; mid-elevation peak; species richness

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Abstract

IPCC predictions for Honduras indicate that temperature will increase by up to 3–6°C and precipitation will decrease by up to 7–13% by the year 2050. To better understand how fern and lycophyte communities might be affected by climate change, we comprehensively surveyed the community compositions of ferns and lycophytes at Celaque National Park, the highest mountain in Honduras. We surveyed a total of 80 20 × 20 m^2 plots along an altitudinal gradient of 1249–2844 m a.s.l., identifying all species and estimating their abundances. We recorded a total of 11,098 individuals from 160 species and 61 genera. Community composition was strongly influenced by changes in altitude, precipitation and the abundance of bryophytes (a proxy for air humidity). Of the 160 species, 63 are expected, under a RCP2.6 scenario for the year 2050, to shift their range fully or partially above the maximum altitude of the mountain. Of these, 65.1% are epiphytes. We found that species with narrow altitudinal ranges at high altitudes were more at risk. Our study indicated that conservation efforts should prioritise higher altitudinal sites, focusing particularly on preserving the vulnerable epiphytic fern species, which are likely to be at greater risk.

Introduction

Mountains are ideally suited to study the effect of climate change on species distributions due to their rapid variability of climate over short altitudinal distances (Kessler *et al.* 2016; Rogora *et al.* 2018). In addition, these geographic features often harbour a very diverse and unique assemblage of fauna and flora and form regional biodiversity hotspots of high conservation importance (Lomolino 2001). Many of these species have discrete altitudinal distributions, determined partially by their biology and the historical distribution of each species, amongst other factors (Watkins *et al.* 2006). Current evidence suggests that plant species ranges have seen an average increase of approximately 30–36 m upwards along altitudinal gradients over the last 10 years, an affect that can be attributed to climate change (Jump *et al.* 2012; Lenoir *et al.* 2008; Morueta-Holme *et al.* 2015). Projections suggest that under a 1.5°C increase scenario, we can anticipate further upward shifts in altitude and a loss of >50% of the geographic range of 8% of plant species by the year 2030 (IPCC 2018). Tropical locations, in particular, are believed to show exacerbated effects of climate change on altitudinal distribution patterns, largely due to the narrow optimal temperature ranges of tropical species (Feeley & Silman 2010), with beneficial effects for some species and detrimental results for others (Gibson-Reinemer & Rahel 2015).

Upslope shifts have potentially negative implications for future diversity, by increasing the risk of extinction for species that occupy high-altitude sites and that have a narrower range size (Colwell *et al.* 2008). As such, altitudinal distribution patterns have been studied for several decades, with particular focus on tropical forest vegetation (Cardelus *et al.* 2006; Ibisch *et al.* 1996; Kessler 2001; Kidane *et al.* 2019; Krömer *et al.* 2005; Rahbek 1995; Richards 1952; Wolf 1993; Zhou *et al.* 2019). However, many Central and South American studies have mostly focused on countries such as Costa Rica (Stroud & Feeley 2017), whilst other areas, including Honduras, have been largely neglected, making generalisations on the effect of climate change on species altitudinal distributions difficult. In particular, the limited attention that Honduras has received has also been restricted to a small number of taxonomic groups. The greatest concentration of these studies in Honduras has focused on birds (Jones *et al.* 2020; Neate-Clegg *et al.* 2018), with fewer studies investigating invertebrates (Anderson & Ashe 2000) and plants (Imbach *et al.* 2013).

Ferns and lycophytes are especially vulnerable to increased temperatures and decreased precipitation, which are both predicted under future climate change, and their responses to these

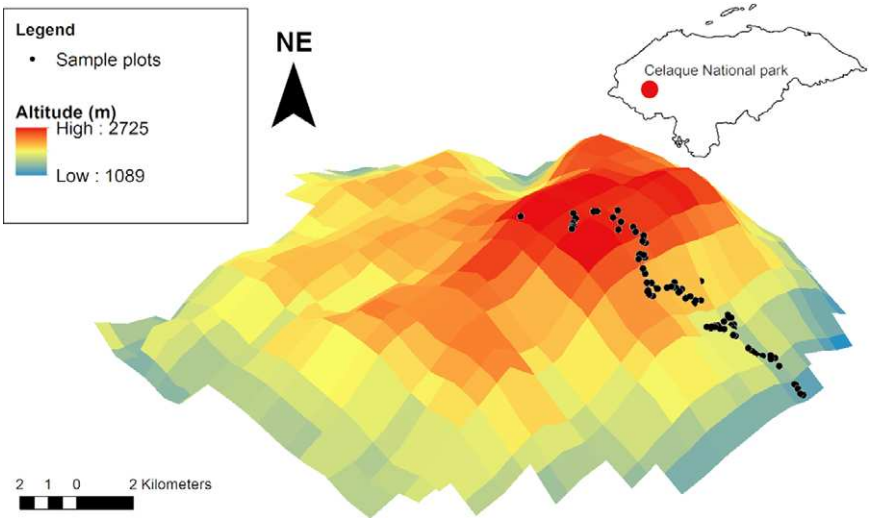

Figure 1. Digital elevation model (DEM) of Celaque National Park. Points show the sample locations ($n = 80$).

conditions will likely differ between terrestrial and epiphytic species (Mandl *et al.* 2010). As a result, this climate sensitive, globally distributed and diverse group of plants has received substantial attention in the literature on global altitudinal distribution pattern studies; both directly (Kessler *et al.* 2001; Kluge & Kessler 2011; Mandl *et al.* 2010; Watkins *et al.* 2006) and indirectly (Sánchez-González *et al.* 2010). However, there is still a severe lack of available distribution data for ferns and lycophytes from some Central American countries such as Honduras, and there is currently no specific distributional data available for epiphytic ferns and lycophytes from anywhere in Honduras. For example, epiphytes until now have only been exclusively studied in Honduras in the context of disturbance events (Batke & Kelly 2015) and biogeographical comparisons (Batke *et al.* 2016). This is a concerning realisation when considering that Honduras contains a high percentage of vascular epiphytes relative to the overall flora of the country (e.g. >30% of 908 vascular plant species in Cusuco National Park) and compared to other Central America countries (Batke *et al.* 2016).

In contrast to the geographical limitations of plant altitudinal distribution research in Honduras, the theory behind the migration of plants upwards along altitudinal gradients has been well established elsewhere. It is believed that climate warming offers more optimal conditions that favour the establishment and survival of plant species at the upper limits of their temperature ranges (Adams & Kolb 2005), effectively resulting in an upslope 'march'. Other theories have also been used to explain upslope plant shifts, such as the synchronous 'lean' response, although these hypotheses are not mutually exclusive and may occur in sequence or combination (Breshears *et al.* 2008). However, the individual response of particular plant groups has been shown to vary greatly (Grau *et al.* 2007, 2011; Wolf *et al.* 2016). For example, epiphytes, which are restricted to life in the canopy, are often separated from the terrestrial soil environment (Zotz & Hietz 2001; Zotz *et al.* 2001) and have been suggested to therefore respond very differently compared to terrestrial plants (Nervo *et al.* 2019); particularly as epiphytes are also highly sensitive to changing climate conditions (Ellis 2013; Ellis & Coppins 2007, 2009, 2010; Hsu *et al.* 2012; Zotz & Bader 2009). Thus, the lack of altitudinal distribution data on terrestrial and epiphytic ferns and lycophytes from Honduras currently prevents us to compare plant distributional responses to predicted changes in future climate to other biodiversity hotspots (Marchese 2015; Myers *et al.* 2000).

To improve our understanding of fern community assemblages across the greatest altitudinal range in Honduras, in this study, we (1) investigated for the first time how species richness, diversity, and community composition patterns of ferns and lycophytes changes along an altitudinal gradient on the highest mountain in Honduras, (2) tested whether there are differences within these patterns between epiphytes and terrestrial species, (3) attempted to identify the underlying environmental factors that drive these patterns, and (4) identified which species are likely to be at greater risk under predicted changes in climate. It is hoped that the data from this study can help us to better understand and generalise the effect of future changes in climate on plant distributions in tropical mountain forests.

Methods

Study site

Celaque Mountain National Park (14°32′08″N, 88°42′26″W) is located within the western region of Honduras, between the departments of Copán, Lempira, and Ocotepeque (Figure 1). The term 'Celaque' comes from the Lenca word 'Celac', which means 'cold water' or 'ice water' and is a reference to the large quantity of flowing water in the park (Flores *et al.* 2012). The protected area contains the highest mountain in Honduras, with an altitude of 2849 m above sea level (a.s.l.).

The topography in Celaque is rugged with sandy and shallow soils (Archaga 1998). The vegetation community classification has not been well defined, but it has been broadly described as *Pinus-Quercus* (pine-oak) forest at lower altitude and transitional mixed broad-leaf/pine montane forest at middle to upper altitude. Above 2200 m, the transitional forest gives way to mainly broad-leaved species (Archaga 1998; Southworth *et al.* 2004). Celaque is believed to be one of the most biologically important sites for plants in Honduras due to its high degree of endemism and diversity (Hermes *et al.* 2016; ICF 2016). With 217 species recorded to date, ferns species are particularly abundant in Celaque. It is believed to be the most species-rich nature reserve in the country for this group (Chávez *et al.* 2020; Reyes-Chávez *et al.* 2018; Rojas-Alvarado 2012, 2017), with two of the seven known Honduran endemic fern species occurring there.

Plot selection

We surveyed a total of 80 20 × 20 m^2 (400 m^2) plots between August 2018 and July 2019, along an altitudinal gradient of 1595 m (1249–2844 m a.s.l) (Figure 1). Every 100 m in altitude, we selected five plots using a stratified random design, focusing on the most representative forest types including ravines and riparian zones, but excluding canopy gaps, landslides, or other highly disturbed areas where possible. Between 2200 and 2400 m, the topography of Celaque was very steep (an approximate slope of 60%), which made it unsafe to sample plots at 2300 m. In each plot, we surveyed fern and lycophyte richness and abundance (by counting every individual in each plot) following Kessler & Bach (1999) and Karger *et al.* (2014). For species with long rhizomes, individuals were counted by identifying clumps, which most likely represented genets. We collected epiphytes by searching for low hanging individuals or fallen branches, as well as a visual search using binoculars from a suitable vantage point.

We identified all ferns and lycophytes to species. Where necessary, we collected voucher specimens for further analysis and verification. In the case of the genus *Elaphoglossum* Schott ex J. Sm., we collected a sample of each morphospecies for closer laboratory examination and counted the number of each type found in each plot.

For each plot, we measured inclination using a clinometer and estimated the amount of soil covered by plants or rocks and total cover of bryophytes on canopy branches as a proxy for air humidity (Karger *et al.* 2012). Percentage soil covered by plants or rocks and total bryophyte cover were visually estimated in the field to the nearest 5%. All estimations were carried out by the same individual.

All the samples were deposited at EAP herbarium of Zamorano University, Honduras. Collections were identified using *Flora Mesoamericana* (Moran 1997), *The Pteridophytes of Mexico* (Mickel & Smith 2004), and other relevant publications (Gonzales & Kessler 2011; Rojas-Alvarado 2003). We followed PPGI (2016) and Hassler & Schmitt (2020) for species classification.

Data analysis

A digital elevation model (DEM) of the park was created using a 50-m contour map. The model was created using scene in ArcGIS 10.8 (ESRI 2020).

The community data were visualised using nonmetric multidimensional scaling (NMS), and Simpson diversity was calculated with the R 'vegan' package (R Developing Core Team 2020). To identify the most important response variable that affected Simpson diversity and fern/lycophyte community composition in Celaque, the Simpson diversity and NMS community scores were correlated in a random/mixed-effects meta-regression model with all response variables. We used the 'glmulti' package in R for this analysis (R Developing Core Team 2020). We fitted the meta-regression model separately for NMS axis 1 and 2. In addition, Simpson diversity was also separately fitted for epiphyte and terrestrial species. The relative model average importance of each variable was plotted and the best-fit model selected using Akaike's information criterion (AIC) (Batke & Kelly 2014). We used a 0.8 cut-off to differentiate between important and less important variables (Calcagno & de Mazancourt 2010). In order to assess the richness distribution of terrestrial and epiphytic species along an altitudinal gradient, a spline regression was fitted with a series of polynomial segments using R (Bruce *et al.* 2020; R Developing Core Team 2020).

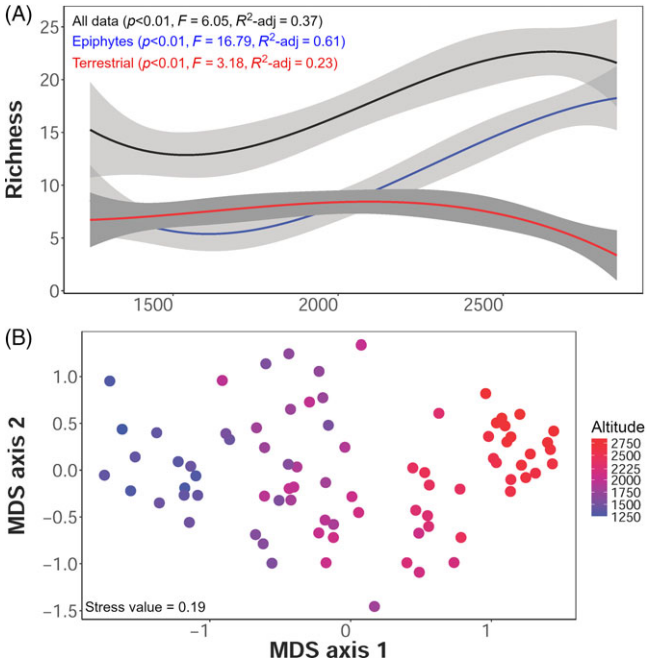

Figure 2. Plot species richness along an altitudinal gradient in Celaque National Park, Honduras (A). Spline regression was fitted with a series of polynomial segments. The mean (solid lines) and standard error (grey shading) are shown only for visualisation purposes. Multidimensional scaling of the community composition data (all life forms) was used to identify community similarities between altitudinal plots ($n = 80$) (B). Panel B shows a two-dimensional ordination of axis 1 and 2 with individual plots highlighted by different colours based on their altitude (blue to red = low to high altitude).

We extracted current temperature and precipitation data for Celaque from Karger *et al.* (2017) and climate predictions for temperature and precipitation for western Honduras for the years 2050 and 2100 for RCP2.6 and RCP8.5 from the *Fifth Assessment Report* (IPCC 2014). To assess altitudinal shifts, as expected from warming and decreases in precipitation, we calculated the lapse rates following Burt & Holden (2010). For each species, we used the rearranged fitted linear equations for the temperature and quadratic equations for the precipitation projections (i.e. solving for x), to calculate altitudinal changes for temperature and precipitation of each climate scenario and year, respectively. We then calculated the number of species that lost all or some of their altitudinal range for each year and climate change scenario. A full loss of range was defined when the minimum altitude of a given species exceeded that of the highest point of the mountain (i.e. 2849 m).

Results

We recorded a total of 11,098 individual ferns and lycophytes from 160 species and 61 genera (Supplementary Material – Table S1). Of the 11,098 individuals, 7,036 were epiphytes (78 species) and 4,062 were terrestrial plants (82 species). The five species with the highest abundance were *Elaphoglossum latifolium* (Sw.) J. Sm. (527 individuals), *Blechnum occidentale* L. (394 individuals), *Niphidium crassifolium* (L.) Lellinger (393 individuals), *Pecluma dulcis* (Poir.) F.C. Assis & Salino (370 individuals), and *Polypodium fissidens* Maxon (361 individuals). When analysing both life forms together, species richness were highest at high-altitudinal sites (~2000–2600 m) (Figure 2A). The same pattern was found for

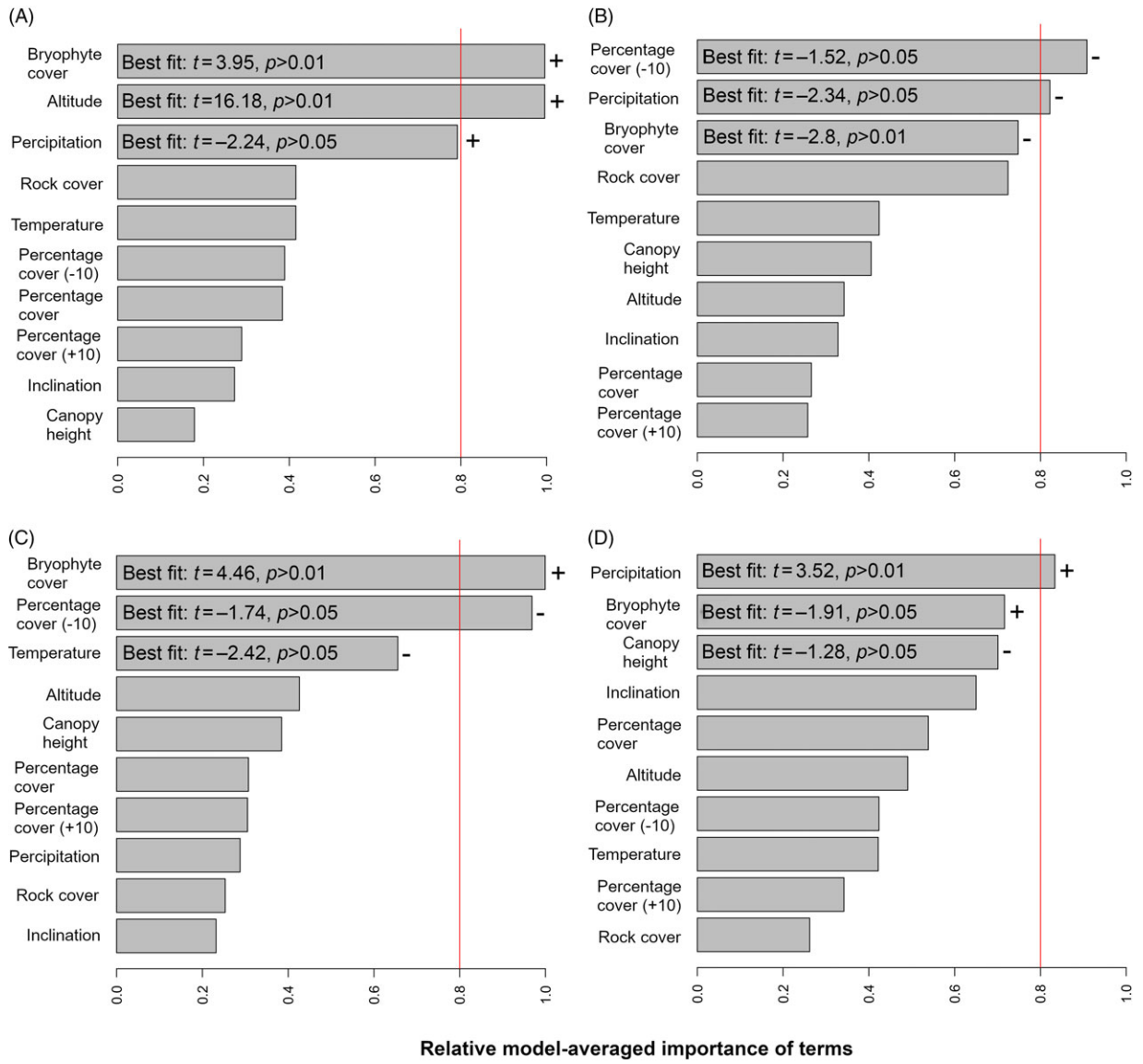

Figure 3. Relative model-averaged importance of terms calculated using a random/mixed-effects meta-regression model for NMS axis 1 (A), axis 2 (B) and Simpson epiphyte (C) and terrestrial diversity (D). The importance for a predictor is equal to the sum of the weights for the models in which the variable appears. The vertical red line is drawn at 0.8 and denotes the cut-off to differentiate between important and less important variables. The model results that are shown for each of the first three variable terms are the best-fit models following AIC selection. The plus and minus symbols denote the direction of the relationships.

epiphytes, whereas terrestrial species had highest richness around ~2000 m, showing a hump-shaped relationship with altitude (Figure 2A).

Current altitudinal range sizes did not differ significantly between epiphytes and terrestrial plants ($p > 0.05$). However, range sizes were proportionally smaller at low- and high-altitudinal sites compared to middle altitudinal sites (not shown).

Community composition in Celaque National Park was strongly influenced by changes in altitude. Higher-altitude sites were floristically different compared to low-altitude sites. An NMS ordination (stress = 0.19) clearly illustrated a transitional change in community similarity along axis 1 (Figure 2B), which was strongly driven by altitude, bryophyte cover, and precipitation (Figure 3A & B; Table 1).

Similarly, Simpson diversity for epiphytes positively correlated to a high abundance of bryophytes, low cover of ground vegetation and low temperatures. It needs to be noted that although ground vegetation cover was an important model factor, it was non-significant for the best-fit model (Figure 3C; Table 1). Terrestrial species diversity on the other hand were positively correlated with high rain fall, high bryophyte cover and low canopy height; however, only precipitation was statistically significant in the best-fit model for terrestrial species (Figure 3D; Table 1). Bryophyte cover was positively correlated with altitude ($F = 14.22$, R^2-adj = 0.55, $p < 0.01$).

Based on IPCC predictions for western Honduras, we are expected to see a temperature increase between 3°C and 6°C and a precipitation decrease between 7% and 13% (Figure 4). Of the 160 species identified, between 7 and 32 species are expected to shift their ranges above the maximum altitude (2849 m) of the highest mountain in Honduras (Supplementary Material Table S1; Table 2; Figure 5). Generally, epiphytes were more negatively affected at high-altitudinal sites compared to terrestrial species due to their narrower range sizes at high altitude and

Table 1. Random/mixed-effects meta-regression model results for the best-fit models, where NMS axis 1 and 2 and Simpson diversity was modelled as a response variable for different explanatory variables. AIC was used to select the best-fit model for each response variable

Response variable	Explanatory variables	Estimate	Std. error	*t*-value	*p*-Value
Axis 1 (AIC = 8.69)	Altitude	0.0017	0.0001	16.18	<0.01
	Bryophyte cover	0.0069	0.0017	3.95	<0.01
	Percentage cover (−10)	−0.0021	0.0018	−1.16	ns
	Precipitation	0.0014	0.0006	2.24	<0.05
Axis 2 (AIC = 115.86)	Bryophyte cover	−0.0081	0.0029	−2.80	<0.01
	Rock cover	−0.0060	0.0031	−1.96	ns
	Percentage cover (−10)	−0.0052	0.0034	−1.52	ns
	Precipitation	−0.0023	0.0010	−2.33	<0.05
Simpson epiphytes (AIC = 117.22)	Bryophyte cover	0.0157	0.0035	4.46	<0.01
	Percentage cover (−10)	−0.0064	0.0037	−1.74	ns
	Temperature	−0.0753	0.0311	−2.42	<0.05
Simpson terrestrial (AIC = 111.59)	Bryophyte cover	0.0058	0.0030	1.91	ns
	Canopy height	−0.0105	0.0082	−1.28	ns
	Percentage cover	0.0063	0.0038	1.69	ns
	Inclination	0.0076	0.0047	1.63	ns
	Precipitation	0.0034	0.0010	3.52	<0.01

Table 2. Number of species per life forms for each year and climate change scenario that are likely to loss part or all of their range

Range lost	Life form	2050		2100	
		RCP2.6	RCP8.5	RCP2.6	RCP8.5
None	Epiphyte	37	37	29	23
	Terrestrial	60	61	54	40
	Sub-total	97	98	83	63
Some	Epiphyte	37	37	31	35
	Terrestrial	19	18	19	31
	Sub-total	56	55	50	66
All	Epiphyte	4	4	18	20
	Terrestrial	3	3	9	11
	Sub-total	7	7	27	31
	Total	160	160	160	160

negative association with higher air temperatures (Table 1; Figure 3C). The percentage mean altitudinal range lost was between 10% and 18% higher in epiphytes compared to terrestrial ferns. For example, of the eight known Hymenophyllaceae Mart. (filmy ferns) epiphytes found in this study, four would lose 100% of their suitable habitat range, whereas another two would lose between 9% and 87% of their range.

Discussion

There has been limited research into the altitudinal distribution patterns of epiphytic and terrestrial fern and lycophytes along mountain ranges, especially in the context of climate change. To our knowledge, our study is the first to explore these changing patterns in Honduras. Understanding plant distribution patterns and identifying the most vulnerable species under future predicted change in climate along altitudinal gradients is important, as it has been shown that high-altitude species are particularly vulnerable under rising atmospheric temperatures (Freeman *et al.* 2018). Increased atmospheric temperatures and decreased water availability from changes in precipitation and cloud formation have been suggested to exacerbate species losses in high-altitudinal sites (Still *et al.* 1999), due to a loss in suitable habitat conditions for those species that have a small–high altitudinal range. These changes in climate are particularly relevant to mountain systems, which exhibit rapid changes in environmental conditions across an altitudinal gradient (Rogora *et al.* 2018), relative to their specific geographic region (Kessler *et al.* 2016), with evidence to suggest that mountains offer an 'elevator to extinction' for high-elevation species (Freeman *et al.* 2018).

Previous studies that investigated the effect of climate change on plant distributions in mountains have often focused on non-tropical mountain biomes, including temperate (Allen & Lendemer 2016; Janssen *et al.* 2019), Mediterranean (Di Nuzzo *et al.* 2021), alpine (Saiz *et al.* 2021) and subtropical localities (Song *et al.* 2012). Fewer studies have specifically focused on tropical locations (Acevedo *et al.* 2020; Hsu *et al.* 2014; Pouteau *et al.* 2016), and with even less data are available for biodiversity hotspots in Central or South America (Acevedo *et al.* 2020). In addition, the altitudinal distribution of selected groups of epiphytes in these understudied tropical montane regions, specifically for epiphytic ferns and lycophytes, remain vastly underexplored (Pouteau *et al.* 2016), making comparisons difficult between Honduras and other localities.

We document here, for the first time, the altitudinal distribution patterns of epiphytic and terrestrial ferns in Honduras along the highest mountain in this country. Our study shows that epiphytes along this mountain exhibit small–high altitudinal ranges. This narrow range has important implications for epiphyte survival, resulting in a greater risk of extinction under future predicted changes in climate, as the ranges of some of these species are likely to shift beyond the maximum elevation of the mountain. For instance, we found that, although species of both epiphytic and terrestrial life forms with narrow range sizes are at high risk in Celaque NP under future IPCC predictions for Honduras, epiphytes were more vulnerable. This is attributed to the higher species richness and abundance of epiphytes at high-altitude plots (ca. 2466–2866 m) under current climate conditions, compared to terrestrial species, which had a higher abundance and richness at mid-altitude. As a result, of the 63 species identified to be at risk (partial or total loss of range) under RCP2.6 for the year 2050, 65.1% were epiphytic taxa, despite epiphytes making up less than 50% of all species recorded. The higher richness in epiphytes at high-elevation sites is thus likely to make them more vulnerable to change in climate conditions, due to their differences in response to environmental conditions compared to terrestrial species

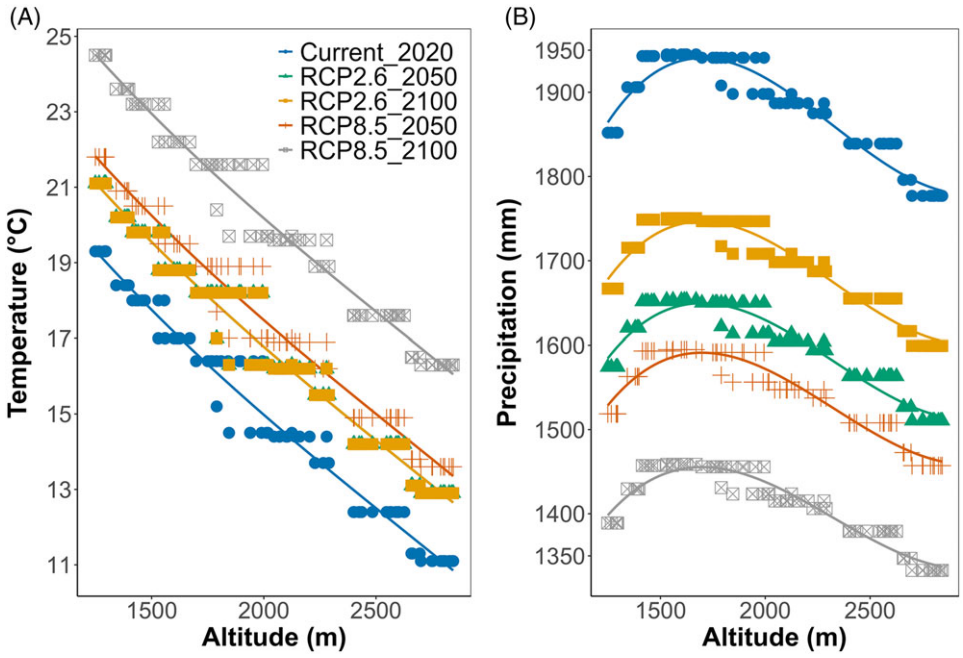

Figure 4. Mean annual temperature (A) and precipitation (B) for the 80 sample locations at Celaque National Park, Honduras. Current mean annual temperature and precipitation was extracted from Karger *et al.* (2017). Climate projections of western Honduras for the years 2050 and 2100 were extracted from IPCC (2014). Current = blue dots; RCP2.6 for 2050 = green triangles; RCP2.6 for 2100 = yellow squares; RCP8.5 for 2050 = orange pluses; RCP2.6 for 2050 = grey squares with a diagonal cross.

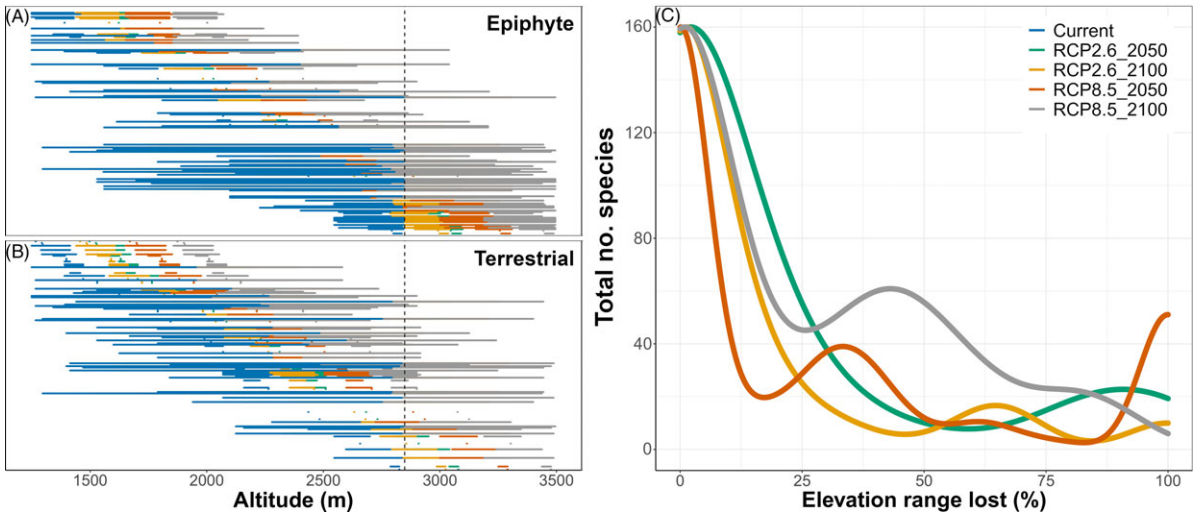

Figure 5. Current and projected species altitudinal ranges for RCP2.4 and 8.5 for the year 2050 and 2100 separated between epiphytic (A) and terrestrial species (B). Each horizontal line represents a single species. For visualisation purposes, the species names are not shown on the y-axis for panel A and B. The vertical dashed line shows the maximum altitude of the mountain. Panel C shows the density distribution of the percentage altitudinal range lost for each scenario and year, weighted by the number of species. Current = blue; RCP2.6 for 2050 = green; RCP2.6 for 2100 = yellow; RCP8.5 for 2050 = orange; RCP2.6 for 2050 = grey.

(Benzing 1990) and their closer range proximity to the maximum elevation of the mountain. Similar results were reported from studies on other vascular and non-vascular species (Zotz & Bader 2009). For instance, many epiphytic ferns are anchored in the forest canopy with no direct connection to the terrestrial soil environment, relying on dead organic canopy matter for nutrients and rain or atmospheric water vapour for moisture input (Benzing 1998; Foster 2001; Hsu *et al.* 2014; Zotz & Bader 2009). Terrestrial species on the other hand are intimately connected to the forest soil through their root system and thus rely much less on atmospheric moisture and canopy organic substrata for their water requirements and nutrient uptake.

Our study demonstrated that 7–31 species of lycophytes and ferns are likely to lose 100% of their range between 2050 and 2100. Epiphytic ferns, however, are likely to have a higher loss of species compared to terrestrial ferns due to their higher predicted range loss (i.e. 10–18% more than terrestrial species). Global simulation of 2°C increase in temperature by 2100 has been predicted to result in the loss of over half the range of 16–57% of plant species (Smith *et al.* 2018; Warren *et al.* 2018), suggesting that our findings are for some species above the global average. We found that particularly, epiphytic ferns that require a continuous water supply, such as species of the genus *Hymenophyllum* Sm. (Hymenophyllaceae), are predicted to be of greater risk.

Hymenophyllum species are found abundantly in humid tropical forests and have been characterised as shade plants, which are well adapted to low light but require ample water supply (Evans 1964; Richards & Evans 1972). These species are considered good indicators of high atmospheric humidity (Hietz & Hietz-Seifert 1995) and due to their dependency on moist habitats, they are extremely sensitive to water loss because of their single-layer cell structure and lack of a well-developed cuticle and stomata (Proctor 2003).

The higher species richness of epiphytes at a higher altitude in Honduras is likely the result of increased precipitation and more continuous water supply (McAdam & Brodribb 2012; Nervo *et al.* 2019). Epiphytic species that are sensitive to water availability appeared to favour higher altitudinal sites, with lower-temperature conditions, increased cloud formation and a supply of fine and frequent precipitation compared to low-altitudinal sites (Bhattarai *et al.* 2004; Frahm & Gradstein 1991). This was demonstrated by the change in community composition along the altitudinal gradient, with a higher prevalence of epiphytic bryophytes at higher-altitudinal plots in our study. Thus, future predicted changes in climate may alter the suitability of these conditions for climate-sensitive epiphytes in Honduras, both directly by changes in climate and indirectly by likely decreases in moisture availability through the bryophyte branch communities. Bryophytes, specifically, can be important for the survival of epiphytic ferns, as increased bryophyte cover facilitates epiphyte establishment (Winkler *et al.* 2005) as well as water interception and storage (Ah-Peng *et al.* 2017; Oishi 2018). In addition, water availability is an important aspect in the fern life cycle as well as for the survival of mature plants, which have less specific stomatal control than angiosperms (McAdam & Brodribb 2013).

Comparisons with previous studies of altitudinal distribution patterns in relation to climate change are challenging due to the complete lack of studies within Honduras and limited studies that investigated tropical epiphytic ferns and lycophytes. Interestingly, we found that epiphyte richness was particularly high at high-elevation sites, which we believed was one of the key driving factors for epiphytes exhibiting a higher range loss compared to terrestrial species under future predicted changes in climate. In comparison, other studies that investigated vascular epiphyte richness along mountains often found a mid-elevation peak in species richness (Hsu *et al.* 2014; Pouteau *et al.* 2016). Therefore, it is likely that the underlying distribution patterns of ferns and lycophytes at a given site will ultimately determine the severity of climate change on the specific life form ranges (e.g. epiphytes vs. terrestrial species).

In conclusion, higher temperatures under future predicted climate change may contribute to increases in total canopy evapotranspiration (Calanca *et al.* 2006; Jung *et al.* 2010), particularly at higher altitudinal sites. With climate change forecasts predicting rising global temperatures and decreases in precipitation (IPCC 2014), tropical montane forests are likely to experience reductions in cloud immersion due to a shift in cloud layers (Foster 2001; Karmalkar *et al.* 2011; Lawton *et al.* 2001; Still *et al.* 1999). These indirect effects of changing climatic conditions have the potential to exacerbate epiphyte species upward range shifts in the tropical montane forests of Honduras (Nadkarni & Solano 2002), as demonstrated in our study. To minimise the potential negative effect of these upward range shifts under future changes in climate, at least at a local and regional level, current conservation strategies in Honduras would require drastic conservation interventions (e.g. assistant migration and ex situ conservation methods) in order to ensure the survival of many of these high-altitude species. However, a lack of robust information on the distribution of ferns across most of Honduras exacerbates the problem. This issue must be addressed as climate change-induced species responses will ultimately affect plant community composition and distributions in Honduras and elsewhere. The highest mountain in Honduras studied here, has and will in the future, provide insight for the first time into how quickly plant communities will respond to changes in climate. Our study has already indicated that specifically high-altitude fern communities in Celaque will change and/or disappear, and it is likely that similar responses threaten species elsewhere.

Supplementary material. To view supplementary material for this article, please visit https://doi.org/10.1017/S0266467421000122

Acknowledgements. We are incredibly grateful to the MAPANCE management team, especially to Hermes Vega for the logistic support during the field trips. We would like to thank Eric van den Berghe and Rina Díaz-Maradiaga from the EAP Herbarium at Zamorano University, Thom Dallimore from Edge Hill University, Katie Kay, David Wright and Klaus Wiese from the Universidad Nacional Autónoma de Honduras for their invaluable advice during the project. We would like to thank Farlem España, Enrique Segura, Juan Rodriguez, Ali Rubio, Nicole Sikkafy, Lodwin Onil and Cristopher Antunez for their help during the data collection.

Funding. This project was supported by the Rufford Foundation (grant number 23585-1), by Idea Wild with an equipment grant to JRC and by an Edge Hill University Research Invest Fund to SPB.

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